


Phenotypic Signals of Sexual Selection and Fast Life History Dynamics for the Long-Term but Not Short-Term Mating

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Abstract

Mating patterns are crucial for understanding selection regimes in current populations and highly implicative for sexual selection and life history theory. However, empirical data on the relations between mating and reproductive outcomes in contemporary humans are lacking. In the present research we examined the sexual selection on mating (with an emphasis on Bateman's third parameter – the association between mating and reproductive success) and life history dynamics of mating by examining the relations between mating patterns and a comprehensive set of variables which determine human reproductive ecology. We conducted two studies (Study 1: N = 398, Study 2: N = 996, the sample was representative for participants' sex, age, region, and settlement size). The findings from these studies were mutually congruent and complementary. In general, the data suggested that short-term mating was unrelated or even negatively related to reproductive success. Conversely, long-term mating was positively associated with reproductive success (number of children in Study 1; number of children and grandchildren in Study 2) and there were indices that the beneficial role of long-term mating is more pronounced in males, which is in accordance with Bateman's third principle. Observed age of first reproduction mediated the link between long-term mating and number of children but only in male participants (Study 2). There were no clear indications of the position of the mating patterns in human life history trajectories; however, the obtained data suggested that long-term mating has some characteristics of fast life history dynamics. Findings are implicative for sexual selection and life history theory in humans.

Keywords

short-term mating, long-term mating, fitness, reproductive ecology, sexual selection, life history theory

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Introduction

Variations in Human Mating Patterns

Differential reproductive success is a central driver of natural selection and thus, one of the main features of biological evolution itself. However, in order to reproduce, individuals must first mate – in many species this does not mean simply finding a partner for reproduction but courting, competing for a mate, retention of a mate, etc. Humans show high variability in their mating patterns cross-culturally, as evidenced by monogamous, polygynous, polyandrous, and polygynandrous mating practices (Wilson et al., 2017). According to the findings of the Standard Cross-Cultural Sample (SCCS), most of the human societies can be labelled as polygynous (82%), followed by monogamous (17%) while only a small proportion of societies was categorized as polyandrous (1%) (Marlowe, 2000). Monogamy seems prevalent in contemporary human populations, but its spread took

place in a relatively recent phase of human evolution. Monogamous marriages are reliably recorded in ancient Greece and Rome (Scheidel, 2009), however, only in recent centuries they spread across the globe with being normative and legally enforced in many countries (Henrich et al., 2012).

The variation in mating is present not only in human marriage systems but in individual differences in mating behavior as well. Individuals differ in their tendency to have long-term versus short-term partner relationships, extra-pair mating, mate poaching, and mate guarding (Buss, 2006; Buss &

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Schmitt, 2019). Short and long-term mating were thought to be opposite poles of a singular dimension labeled sociosexuality – higher levels of this behavioral tendency depict a tendency toward short term mating and uncommitted relationships (Simpson & Gangestad, 1991). Empirical research showed that males have higher scores on sociosexuality compared to females, in many cultures (Schmitt, 2005). However, more recent research showed that short and long-term mating preferences may not be the opposite poles of the single mating dimension but rather two distinct mating strategies with negative associations between them (Holtzman & Senne, 2014; Jackson & Kirkpatrick, 2007).

Mating in the Context of Sexual Selection

There are at least two important theoretical frameworks that can help us understand the role of mating in fitness maximization. The first one is sexual selection. It is a specific case of natural selection which describes how inter and intra-sexual competition for mates can generate sex-specific mating patterns (Darwin, 1871). One of the main approaches to measuring sexual selection is based on the work of Bateman (1948; see also the recent review with the applications of Bateman's work to sexual selection in humans: Borgerhoff Mulder, in press). This framework posits that the sex which is more affected by sexual selection (most frequently these are males) should exhibit higher variation in mating and reproductive success, and higher covariation between mating and reproduction (Janicke et al., 2016).

There is a possibility that sexual selection is weaker in contemporary, compared to ancestral human populations: as stated before, the dominant pattern of marriage in humans is monogamy while sexual selection in monogamous populations is weaker than in polygamous (Moorad et al., 2011). Monogamy reduces the strength of sexual selection by decreasing intrasexual competition, downsizing the number of males in the mating pool, alleviating the competition for younger brides, and increasing the levels of paternal investment (Henrich et al., 2012). However, despite the magnitude of selection, the existing data show patterns which are congruent with Bateman's predictions. Males have higher variation in mating and reproduction success and more increased fitness by multiple mating in preindustrial Finnish populations (Courtiol et al., 2012), early 20th century US populations (Jokela et al., 2010), and in rural natural-fertility populations in Tanzania (Borgerhoff Mulder & Ross, 2019).

There are data which did not corroborate the third Bateman's coefficient (higher association between mating and fitness in males) as well. A recent study analyzed the relations between short, long-term mating, and several reproductive outcomes (Mededović, 2021). It was found that long-term mating (duration of the longest romantic relationship) positively predicts number of children and grandchildren, but there were no sex differences in the links between long-term mating and reproductive fitness. The absence of sex's moderating role can be explained by the sample structure in abovementioned study:

all participants were parents, hence, the variation in number of children was diminished since no childless individuals were included in the analysis.

Evolutionary psychologists have not empirically analyzed Bateman's gradients directly. They have mostly focused on sex differences in mean levels of mating behavior with the data mostly confirming that males have higher sociosexuality levels than females (Penke & Asendorpf, 2008; Schmitt, 2005). This suggests that males pursue short-term mating, engage in uncommitted relationships with greater frequency, and tend to have a higher number of sexual partners in general. However, this approach is criticized by stating that the mean levels of mating success in males and females should be the same on a population level (Bond, 2005). This is a consequence of Fisher's condition (Kokko & Jennions, 2008) – the fact that copulation and reproduction demand two individuals of the opposite sex (since the main indicator of fitness is reproduction, we do not refer to homosexual partner relationships here). Hence, the findings of higher mean short-term mating success in males could be a consequence of the tendency of males to overestimate their number of sexual partners. Recent analysis of sex differences in mating showed that males and females are probably more similar than different in their mating patterns, with long-term mating being the dominant mating strategy (Stewart-Williams & Thomas, 2013), which is in line with the data indicating a low magnitude of sexual selection in humans.

What Can Mating Patterns Tell Us About Human Life History?

Another theoretical framework with tremendous impact in evolutionary social sciences is life history theory. In order to understand fitness maximization, it is not enough to analyze fitness proxies (i.e. reproductive success) but various fitness components and fitness-related outcomes. The reason is that fitness is a multi-component trait with its components constraining each other: e.g. investing in reproduction prevents investment in longevity (Tabatabaie et al., 2011), offspring quantity is inversely related to offspring quality (Gillespie et al., 2008) and mating impedes parental investment (Gangestad & Simpson, 2000). These are evolutionary trade-offs – their existence forces individuals to generate different pathways towards fitness maximization; these pathways can be described as life history trajectories. Two basic life history pathways are labeled as fast and slow: fast is depicted by earlier maturation, onset of sexual activity, and first reproduction, higher reproductive output followed by lower parental investment and decreased longevity; slow life history is characterized by the opposite pattern (Del Giudice et al., 2015). An additional indicator of fast life history dynamics is reproductive motivation (e.g. higher desired number of children) because it is positively associated with reproductive success and negatively with the age of first reproduction (Mededović, 2021). The emergence of life history trajectories is facilitated by the environmental characteristics: empirical

data reliably show that harsh, unpredictable, hostile, and depriving environments are associated with fast life history dynamics (Chisholm et al., 2005; Dunkel et al., 2015; Griskevicius et al., 2011; Međedović, 2019; Sheppard et al., 2016; Webster et al., 2014). It is assumed that the effect of harsh ecologies on life histories is crucially dependent on the individuals' developmental phase: the potential of environmental harshness to facilitate fast life history trajectories is higher in early and middle childhood, compared to latter ontogeny phases (Belsky, 2012; Del Giudice, 2009). Ecological conditions in childhood influence life history dynamics in adults either by enabling the prediction of future environments (if childhood and adult ecologies are mutually congruent) or by changing the somatic development of individuals towards faster or slower pubertal and reproductive timing (Rickard et al., 2014).

Human behavioral ecologists rarely analyze mating patterns in a life history context; however, the research in evolutionary psychology provide some suggestions of human mating life history characteristics. In fact, there are two opposite hypotheses regarding the relations between mating strategies and environmental characteristics. The first can be labeled the *developmental-attachment theory*: harsh and stressful environments (Belsky et al., 1991) with elevated mortality rates (Chisholm, 1999) would lead to short-term mating strategies since they should be adaptive in such an environment. Quite oppositely, the *strategic pluralism theory* predicts that harsh, depriving, and hostile environments demands biparental care in order to elevate offspring fitness; hence, long-term mating should be adaptive in these ecologies (Gangestad & Simpson, 2000). Generally, the empirical data are mostly in line with the assumption that short-term mating is related to a fast life history since it is negatively related to life expectancy, with positive associations with family instability (Copping & Campbell, 2015). Furthermore, short-mating patterns emerge from harsh and unpredictable community environments via earlier pubertal timing (Kogan et al., 2015). Congruent with these findings, long-term mating is positively associated with parental support (Lukaszewski, 2015) and negatively with family neglect and neighborhood crime (Chua et al., 2016). However, the data on the population level shows the opposite pattern – short term mating positively associates with beneficial ecological characteristics, which is more congruent with the assumptions of the strategic pluralism theory (Schmitt, 2005). Hence, the role of mating patterns in life history dynamics is far from being resolved.

Goals of the Present Research

Analyzing mating behavior is crucial for understanding how individuals and populations achieve and maximize fitness. It is relevant from the position of at least two theoretical frameworks in evolutionary sciences, sexual selection and life history theory, and it has important practical implications, for example in a demographical context (Borgerhoff Mulder, in press). However, the empirical data regarding the relations

between different mating patterns and reproductive fitness are still quite rare. The main goal of the present research is to evaluate the links between mating and fitness in a wider context of human reproductive ecology, by measuring various outcomes which are significant for individual fitness (e.g. age at first reproduction, number of children and grandchildren, having offspring with multiple partners, etc). The data are analyzed and interpreted from the point of view of sexual selection and life history theory. These theories generate exact hypotheses regarding the relations between mating and fitness-related outcomes. In line with the sexual selection theory we calculated interactions between sex, mating, and fitness outcomes - if sexual selection is acting on mating patterns they should show higher associations with fitness in males. Furthermore, we analyzed the relations between mating and other indicators of reproductive ecology in order to evaluate if there are patterns which are congruent with fast/slow life history dynamics. The data was collected in Serbia, a southeast European country which represents WEIRD society (Western, Educated, Industrialized, Rich, and Democratic), although with underdeveloped democratic procedures and lower economic standards (Zemniczky et al., 2015). However, in terms of fertility it reflects a typical population in demographic transition showing below-replacement fertility with the 1.4 live births per woman over a lifetime (United Nations, 2020).

In order to achieve the research goals we conducted two studies, with largely different samples. We measured mating by using the number of sexual partners and the duration of the longest relationship in every study. Usually, mating success is measured by the number of mating partners, especially the number of marriage partners in human behavioral ecological research. However, recently it has been argued that the time spent married is an important measure of mating success since it indicates opportunity for copulation and, consequently, reproduction (Blurton Jones, 2016; Borgerhoff Mulder, 2017; Borgerhoff Mulder & Ross, 2019). This measure of mating success is not limited to formal marriages - even in traditional societies a "marriage" can mean coresidence of sexual partners, shared provisioning and household labor, i.e. long-standing romantic and sexual partnerships (Borgerhoff Mulder & Ross, 2019). This notion of long term-mating is probably even more present in industrial and postindustrial human societies: in contemporary humans, especially in WEIRD countries, there are many romantic partners who are not officially married, but despite this, form long-lasting partner relationships (Uggla & Mace, 2017). Hence, we measured the longest partner relationship in general, regardless of whether it was an official marriage or not. In addition, we explored the total number of sexual partners; we address these two measures as the indicators of long and short-term mating, respectively. As has been recently addressed (Borgerhoff Mulder & Ross, 2019), only by measuring these distinct indicators of mating can we obtain valid information on the role of mating patterns in human reproductive ecology. Hence, in the present research we tried to integrate evolutionary psychological and behavioral ecological approaches to mating into a single research framework.

Study I

Goals of the Study I

The main goal of Study I is to analyze the relations between mating, childhood environment, and reproduction. Furthermore, we aimed to compare the psychometric measures of long and short-term mating with behavioral measures of mating. We expected positive correlations between the short-term mating scale and the number of sexual partners and between the long-term mating scale and the duration of the longest relationship. Additionally, we expected higher associations between mating and reproductive success for males as predicted by sexual selection theory. More precisely, since previous research showed that long, but not short-term mating is positively related to fitness (Međedović, 2021), we expected that this mating behavior may be more beneficial for male compared to female fitness. Finally, psychosocial acceleration theory predicts that short-term mating is a part of fast life history dynamics - hence, it should be positively related to harsher environment, earlier onset of sexual activity and reproduction, higher number of children, and a higher number of desired children; the opposite should stand for long-term mating. Conversely, strategic pluralism theory assumes that long-term mating should be positively related to these life history indicators, i.e. that long-term mating represents a part of fast life history trajectory.

Method

Sample

The data were collected by an on-line study. Students of the evolutionary social science course from the Singidunum university of Belgrade disseminated the link for the on-line survey via social networks and e-mails to informal contacts as a part of their course. They asked the initial participants to find additional participants so the sampling was conducted via the snowballing technique. The purpose of the study and the informed consent form was present on the first page of the survey. This procedure resulted in a convenience sample of 398 individuals of Serbian ethnicity (68% females; $M_{\text{age}} = 31.03$ [$SD = 11.65$]). The participants' education was higher than average: the majority of participants have finished college (44%) or they were attending college at the time of data gathering (43%) with a lower number of participants who finished high school (13%). The majority of participants did not have children (75%). Participation in the research was voluntary for all participants.

Measures

We measured short and long-term mating using the behavioral and psychometric measures¹. The former ones are operationalized as the *Number of sexual partners* and the duration of *Longest (partner) relationship* (expressed in months), respectively. Psychometric measures were operationalized via the items from *short* and *long-term mating* scales of the expanded Sociosexual Orientation Inventory (Jackson & Kirkpatrick,

2007). Every scale was measured via 5 items with the standard Likert-type scale for responding.

In addition, we measured self-reported socio-economic status in childhood (*Childhood SES*) and *Relations in family*: 1) "On a scale of 1 to 10, please evaluate the financial situation in your family while growing up"; 2) "On a scale of 1 to 10, please evaluate the relationships in your family while growing up", respectively. Number 1 was marked "Very bad" while 10 represented "Very good". We also measured the *Age of first sex* with the following question: "How old were you when you had your first sexual intercourse?" *Number of children* was measured via the number of biological children. However, due to a fact that 25% of our participants had children in the time of data collection, we binarized this measure (we coded childless individuals with 0 and participants with children with 1). The age at first reproduction was measured via two items: participants who had children were asked "How old were you when you had your first child?" We refer to this variable as the *Observed age of first reproduction*. If a participant did not have children, the question was: "How old would you like to be to have your first child?" This variable is labeled as *Planned age of first reproduction*. Finally, we asked participants what their total *Desired number of children* is.

The Plan of Data Analysis

The data analysis was conducted in four steps. First we showed descriptive statistics and sex differences on examined measures obtained by t-test. Afterwards, we calculated zero-order and partial correlations between the analyzed variables – this allowed us to estimate if associations between mating patterns and other measures correspond to life history trajectories. In the third step we tested the regression model with a Number of children as a criterion measure. Finally, we explored the interactions between sex and mating in the prediction of the number of children. These last two steps enabled us to estimate the third Bateman's coefficient – the moderating effect of participants' sex on a link between mating and reproduction..

Results

Sex Differences and Correlations Between the Examined Variables

First, we showed sex differences in the examined variables, including the tests for differences in means and variances. These data are shown in Table 1. We can see that males had higher mean scores on both measures of short-term mating, Planned age at first reproduction, and Childhood SES; furthermore, they reported lower values of psychometrically measured Long-term mating. Males also had higher variation (indicated by a significant Levene's test) in the Number of sexual partners and Long-term mating.

We calculated the correlations between the examined variables on the entire sample; Pearson's coefficients of linear correlation are shown for every variable except for the

Table 1. Sex Differences Between the Examined Variables.

| | M(SD) _{males} | M(SD) _{females} | F | t |
|--------------------------------|------------------------|--------------------------|---------|---------------------|
| 1. Number of sexual partners | 11.31(14.02) | 6.20(8.85) | 26.69** | -4.26** |
| 2. Short-term mating | 4.56(1.38) | 3.70(1.36) | 0.06 | -5.84** |
| 3. Longest relationship | 60.12(78.85) | 68.01(90.65) | 0.49 | 0.80 |
| 4. Long-term mating | 5.73(1.03) | 5.96(0.84) | 4.77* | 2.38* |
| 5. Childhood SES | 6.19(2.05) | 6.69(1.77) | 6.43* | 2.49* |
| 6. Relations in family | 6.75(2.46) | 6.89(2.40) | 0.52 | 0.53 |
| 7. Age of first sex | 18.04(2.90) | 18.04(3.64) | 0.02 | -0.02 |
| 8. Number of children | 21% | 24% | / | 0.04 _(c) |
| 9. Observed AFR | 30.08(4.93) | 28.73(5.48) | 1.24 | -1.09 |
| 10. Planned AFR | 30.96(3.64) | 29.05(2.97) | 3.57 | -4.56** |
| 11. Desired number of children | 2.62(0.90) | 2.45(0.83) | 0.78 | -1.74 |

Notes: F - Levene's test for equality of variances; t - t-test for equality of means; _(c) - Contingency coefficient was calculated for the Number of children; * - $p < .05$; ** - $p < .01$.

Reproductive success where a point-biserial correlation coefficient was calculated. Before the correlation analysis, all the measures which did not normally distribute in our sample (including all count measures) were normalized using the Blom algorithm. We calculated both zero-order correlations and partial correlations controlled for participants' sex, age, and education; the correlations in males and females separately are shown in the Supplementary material. These data are presented in Table 2.

Since the participants' sex, education, and especially age are crucial covariates in the examined relations, we interpreted only partial associations. The Number of sexual partners correlated positively with Short-term mating and the Observed age of first reproduction; it was associated negatively with the Age of first sex. Short-term mating had positive correlations with Childhood SES and the Planned age of first reproduction, while it had negative associations with the Age of first sex. Longest relationship correlated positively with Reproductive success and negatively with the Age of first sex. Finally, Long-term mating had negative associations with the Planned age of first reproduction and positive with the Desired number of children. Note that the Longest relationship duration

was not related to Long-term mating. Most of the significant correlations had small to moderate effect sizes.

Sex as the Moderator of the Mating-Fitness Link

We conducted a binary-logistic regression analysis where we set the participants' sex, age, education, Childhood SES, Relations in family, and mating patterns as the predictor variables; Number of children was set as the criterion measure. This procedure resulted in a statistically significant regression model with participants' age, education, and Longest relationship duration as significant predictors; self-reported Short-term mating attitudes had a marginal negative contribution to the prediction. Afterwards, we added the interactions between sex and mating at the second level of the analysis. Only one interaction showed to be significant: Males with longer relationships had elevated Reproductive success, while females with shorter relationships had higher probability to have children. Contributions of the variables to the regression functions and graphic representations of the interactions can be seen in Table 3 (the second column represent the regression model with interaction term included) and Figure 1.

Table 2. Correlations Between the Examined Variables.

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 |
|--------------------------------|--------|--------|--------|--------|-------|-------|--------|-------|------|--------|--------|
| 1. Number of sexual partners | | .30** | .04 | .03 | -.03 | -.05 | -.35** | -.04 | .23* | -.02 | -.01 |
| 2. Short-term mating | .29** | | .03 | .01 | .13* | .02 | -.11* | -.04 | -.06 | .14* | -.03 |
| 3. Longest relationship | .12* | -.09 | | .07 | -.06 | .03 | -.24** | .19** | .03 | -.09 | .04 |
| 4. Long-term mating | -.02 | .00 | .01 | | -.05 | -.04 | -.05 | .01 | -.06 | -.14** | .20** |
| 5. Childhood SES | -.08 | .11* | -.10* | -.02 | | .35** | .05 | -.01 | -.05 | .04 | -.05 |
| 6. Relations in family | -.06 | .02 | .01 | -.03 | .35** | | .08 | -.01 | .05 | -.06 | .00 |
| 7. Age of first sex | -.32** | -.15** | -.14** | -.05 | .04 | .08 | | -.08 | .04 | .04 | -.05 |
| 8. Number of children | .14** | -.22** | .44** | -.07 | -.12* | -.05 | .03 | | -.02 | / | .07 |
| 9. Observed AFR | .28** | .04 | .09 | -.10 | -.09 | .09 | -.02 | -.04 | | / | -.02 |
| 10. Planned AFR | .17** | .17** | .05 | -.17** | -.07 | -.09 | .08 | / | / | | -.28** |
| 11. Desired number of children | .01 | .02 | .00 | .19** | -.06 | .01 | -.07 | -.01 | .05 | -.24** | |

Notes: zero-order correlations are shown below the diagonal; correlations partialized for sex, age, and education are shown above the diagonal; * - $p < .05$; ** - $p < .01$.

Table 3. Interactions Between sex and Mating in the Prediction of Number of Children.

| | B (SE) | B (SE) |
|-----------------------------|--------------|-------------|
| Sex | -0.88(.51) | 0.43(.58) |
| Age | 0.18(.02)** | 0.19(.02)** |
| Education | -0.69 (.30)* | -0.77(.32)* |
| Childhood SES | -0.06(.22) | -0.07(.23) |
| Relations in family | -0.22(.25) | -0.26(.26) |
| Number of sexual partners | -0.00(.27) | -0.01(.28) |
| Short-term mating | -0.49(.27)† | -0.58(.28)* |
| Longest relationship | 0.83(.27)** | 0.34(.32) |
| Long-term mating | -0.17(.23) | -0.24(.24) |
| χ^2 | 239.96** | |
| R ² | .48 | |
| Relationship duration * Sex | | 1.57(.65)* |
| χ^2 | | 6.89** |
| R ² | | .01 |

Notes: † - $p = .07$; * - $p < .05$; ** - $p < .01$.

Discussion

Sex differences in mating obtained in Study 1 are partially in accordance with the previous results: both indicators of short-term mating were more expressed in males – which is the finding observed in various cultures (Schmitt, 2005). Previous research (Jackson & Kirkpatrick, 2007) found negative relations between psychometric operationalizations of short-and

long term mating – but we did not detect associations between these measures. Males and females also differed in variation of sexual partners they had and scores on the scale of long-term mating: variation on both variables was higher in males. This is in accordance with Bateman's first principle (Bateman, 1948) that variance in mating should be higher in the sex which is more affected by sexual selection – in humans, as in the majority of species, these should be males (Borgerhoff Mulder, in press). However, note that we did not confirm Bateman's second observation – reproduction success did not variate in males more than in females. The absence of the effect may be due to the relatively small subsample of participants who had children in the present study. Generally, the diminished variation of the reproductive success in the current sample (which is a consequence of the participants' mean age) represents one of its most important limitations.

Individuals with longer relationships had a higher number of children – this relationship was statistically significant even when participants' sex, age, and education were controlled for in analysis. This is a confirmation of the finding that a higher amount of time spent married is beneficial for fitness (Borgerhoff Mulder & Ross, 2019) and previous data that individuals who had longer partner relationships have higher number of children (Mededović, 2021). Furthermore, long term mating elevated fitness especially in males; conversely was found for females. Previous research also established that mating increases fitness in males more than in females (Courtiol et al., 2012; Jokela et al., 2010), with only one study which showed that long-term,

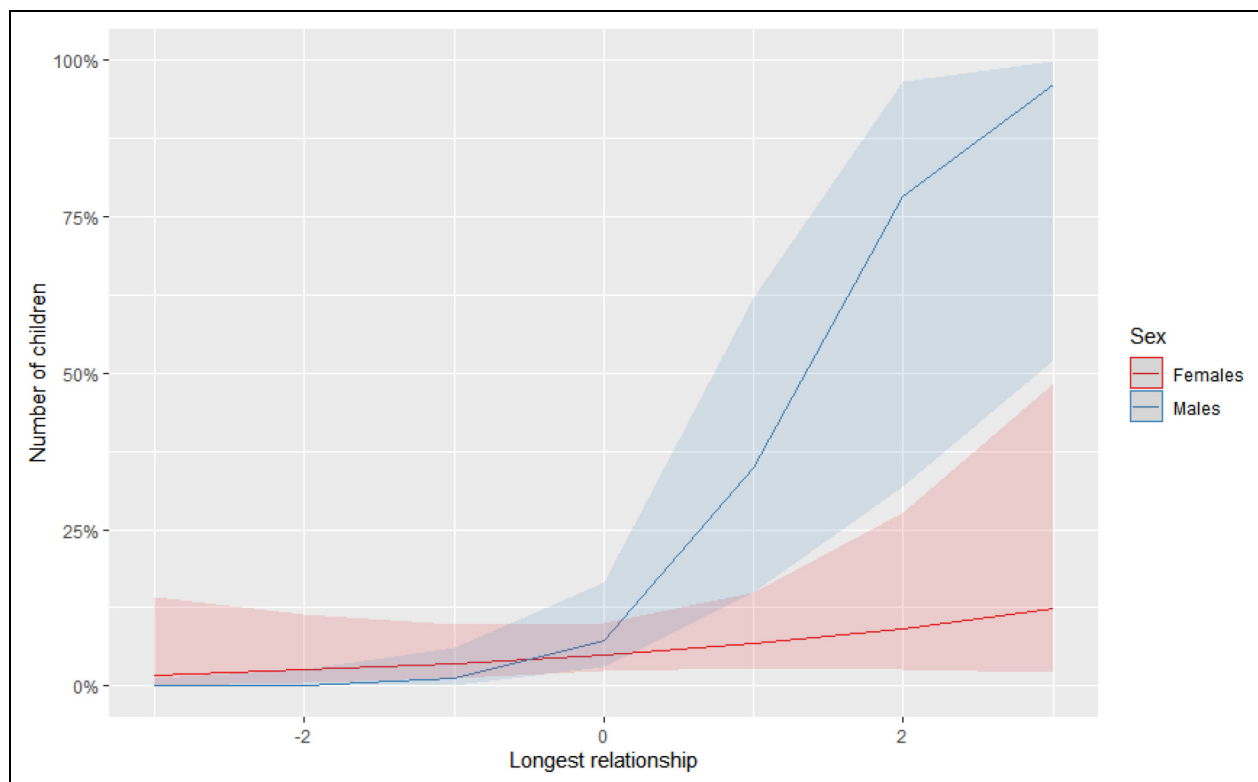


Figure 1. The interaction between sex and long-term mating in the prediction of number of children.

but not short-term mating contributes to male fitness (Borgerhoff Mulder & Ross, 2019). This finding confirms Bateman's third principle that the association between mating and reproduction should be higher in males. The self-report scale which we used for the measurement of short-term mating showed marginally significant negative contributions to the prediction of reproductive success - the finding that we did not anticipate and which suggests that attitudinal proneness to short-term partner relations may even be detrimental for early fitness. It must be noted that we measured early fertility in the present study; this certainly represents its limitation since lifetime reproductive success represent more valid fitness proxy. However, early fertility is still an adequate indicator of completed fertility: one of the crucial predictors of lifetime reproductive success in the age of first reproduction - this association exists both on the phenotypic and genetic level (Sanjak et al., 2018; Troupf et al., 2015). Hence, individuals who have their first child earlier in their lifetime tend to have higher total reproductive success - this is why early fertility is a meaningful indicator of reproductive fitness.

The analysis of mating patterns in the life history context provided inconclusive results. Generally, different mating patterns showed indications of both fast and slow life history. Both indicators of short-term mating showed negative relations with the onset of sexual behavior which may indicate fast life history; however, the number of sexual partners showed positive associations with the observed age of first reproduction, while psychometrically measured short-term mating had positive relations with childhood SES and the planned timing of reproduction, which indicates slow life history. Long-term mating had a more unambiguous position in life history dynamics. Relationship duration had a negative relationship with sexual debut and positive with the number of children; psychometrically measured long-term mating negatively correlated with planned reproduction timing and positively with desired number of children. The pattern of associations suggests that both indicators of long-term mating are associated with fast life history. Hence, this result for long-term mating is more congruent with the strategic pluralism theory (Gangestad & Simpson, 2000), but it should be noted that long-term mating did not positively associate with a harsh environment as predicted by this theory.

Finally, the number of sexual partners was significantly related to the attitudes toward short-term mating which was obtained in previous research as well (Jackson & Kirkpatrick, 2007; Kruger, 2017). However, the duration of the longest relationship was not associated with attitudes toward long-term relationships. This clearly shows the discrepancy between attitudes and behavior - people may want to be committed in long-term romantic relationships, but for various reasons they fail to execute this intent in their behavior. This finding, combined with markedly different relations between psychometrically and behaviorally measured mating patterns and other variables, suggests that these measures do not assess the same concepts. Since we are primarily interested in behaviors, not psychological representations of mating, in the second study we administered only the behavioral indicators of mating.

Study 2

Goals of Study 2

In Study 2 we wanted to further explore the relations between mating, environment and reproductive outcomes. Furthermore, the characteristics of the sample (larger sample size and higher age variation) allowed us to investigate additional parameters of reproductive ecology like the number of grandchildren and having children with different partners. The analytic plan was very similar to Study 1 - analyzing the relations between all variables and the moderation of participants' sex in the mating-fitness link. The assumed fast life history dynamics based on reproductive ecological variables used in the present study should be reflected in elevated environmental harshness, higher reproductive success and higher probability of having children with different partners followed by an earlier age of first reproduction. Furthermore, an additional hypothesis is tested in this study: guided by the previous empirical data (Međedović, 2021) we tested the hypothesis that lower age of first reproduction represents a mediator between long-term mating and fitness. Hence, beside the bivariate associations analysis, prediction of fitness measures, and calculating interactions between sex and mating patterns in the prediction of fitness, we conducted the path analysis in this study as well; this allowed us to test the hypothesis of the age of first reproduction as a mediator in the link between mating and fitness.

Method

Sample

The data was collected through the on-line panel of Deep-Dive, a market research company in Serbia. Potential participants were selected from a database of respondents who are registered as interested to participate in research. Participants were motivated by a voucher that can be used in certain stores. The sample was representative of the general population in terms of the participants' sex, age, region, and settlement size (quota were made according to the 2011 census). A total of 996 subjects (52% females) participated in the study. They were aged 18 to 81 ($M_{\text{age}} = 40.81$, $SD = 12.78$). The distribution of the participants' education was as following: 0.4% did not complete elementary school; 1.2% completed elementary school; 40.8% completed secondary vocational school; 9.6% completed gymnasium; 48% and completed college. The distribution of education showed that participants were more highly educated compared to Serbian average. The measures analyzed in the present report were administered as part of a larger survey. Majority of participants had children (59.9%) with a small proportion of participants who had grandchildren (15.8%).

Measures

Number of sexual partners, Longest relationship, Childhood SES, Relations in family, Number of children, Age of first reproduction (both planned and observed) were measured exactly as in Study 1 (however, Number of children is operationalized as a

Table 4. Sex Differences Between the Examined Variables.

| | M(SD) _{males} | M(SD) _{females} | F | t |
|---------------------------------------|------------------------|--------------------------|----------|------------------------|
| 1. Number of sexual partners | 8.47(9.05) | 3.39(4.45) | 150.30** | -11.10** |
| 2. Longest relationship | 11.95(12.51) | 9.47(8.91) | 84.84** | -3.56** |
| 3. Childhood SES | 5.54(2.28) | 5.09(2.17) | 1.48 | -3.20** |
| 4. Relations in family | 3.77(2.37) | 3.79(2.39) | 0.07 | 0.08 |
| 5. Number of children | 1.37(1.19) | 0.93(1.02) | 10.66** | -6.28** |
| 6. Number of grandchildren | 24.7% | 7.50% | / | 0.23 _(c) ** |
| 7. Children with different partners | 5.40% | 2.50% | / | -0.08 _(c) * |
| 8. Planned age of first reproduction | 33.97(7.70) | 31.24(5.58) | 15.87** | -3.80** |
| 9. Observed age of first reproduction | 28.20(5.35) | 26.82(5.05) | 0.06 | -3.20** |

Notes: F - Levene's test for equality of variances; t - t-test for equality of means; _(c) - Contingency coefficients was calculated for the Number of grandchildren and Children with different partners; * - $p < .05$; ** - $p < .01$.

continuous measure in this study). In addition, we asked the participants for the *Number of their grandchildren* and if they had *Children with different partners*. Due to a relatively small proportion of participants who had grandchildren and children with different partners (3.9%), these measures were binary-coded in the present study.

The Plan of Data Analysis

Data were analyzed similarly to the ones in Study 1: we explored sex differences in analyzed measures and correlations between the measures; afterwards we tested regression models for the prediction of reproductive success and the interactions between sex and mating in these models. However, we conducted two multiple linear regression models in this study - for the Number of children and Number of grandchildren. Finally, we had an additional analytical step in Study 2 - we explored the path analysis where Age of first reproduction was set as the mediator of the link between mating patterns and reproductive success measures.

Results

Sex Differences and the Correlations Between the Examined Measures

First, we show the differences between males and females on analyzed measures (Table 4). The findings showed a clear pattern:

males had both higher variation and mean scores on the Number of sexual partners, Longest relationship, Age of first reproduction (males had higher means on both planned and observed Age of first reproduction but the variation was significantly different only on the former measure), and Number of children. Similarly, the higher percentages of males had grandchildren and children with different partners, compared to females. Bivariate associations between the analyzed measures are shown in Table 5 (the correlations in males and females separately are shown in the Supplementary material). The Number of sexual partners was negatively associated to the Number of children while the Longest relationship was positively associated both with number of children and grandchildren and negatively with the Observed age of first reproduction (note that we interpreted only the correlations partialized for participants' sex, age, and education, similarly as in Study 1).

Moderators in the Mating-Fitness Link

We ran multiple linear regression models for the Number of children and grandchildren as the criteria variables; participants' sex, age, education, childhood environmental characteristics, and mating patterns were set as the predictors. Participants' sex, age, and Longest relationship had positive contributions to the prediction of the Number of children, while education and Number of sexual partners had negative contributions to the regression function (Table 6). We tested

Table 5. Correlations Between the Examined Variables.

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 |
|---------------------------------------|-------|--------|-------|-------|--------|--------|--------|------|--------|
| 1. Number of sexual partners | | -.03 | -.01 | .02 | -.10* | -.05 | .08 | .07 | .07 |
| 2. Longest relationship | .01 | | .02 | -.03 | .13** | .23** | .00 | -.00 | -.10* |
| 3. Childhood SES | .03 | -.00 | | .48** | -.01 | .05 | -.07 | -.05 | .02 |
| 4. Relations in family | .01 | -.09** | .48** | | .03 | .01 | .06 | .01 | -.01 |
| 5. Number of children | .02 | .40** | .01 | -.04 | | .14** | .28** | / | -.31** |
| 6. Number of grandchildren | .06 | .41** | .07* | -.04 | .39** | | -.01 | .02 | -.29** |
| 7. Children with different partners | .08* | .09** | -.04 | .03 | .29** | .08* | | / | -.13** |
| 8. Planned age of first reproduction | .22** | .21** | -.10 | -.08 | / | .12* | / | | / |
| 9. Observed age of first reproduction | .12** | -.05 | .03 | -.02 | -.30** | -.18** | -.13** | / | |

Notes: zero-order correlations are shown below the diagonal; correlations partialized for sex, age, and education are shown above the diagonal; * - $p < .05$; ** - $p < .01$.

Table 6. Interactions Between sex and Mating in the Prediction of Number of Children and Number of Grandchildren.

| | Number of children | Number of grandchildren | |
|-------------------------------|--------------------|-------------------------|------------|
| | β (SE) | B (SE) | B(SE) |
| Sex | .08(.05)** | .78(.28)** | .42(.31) |
| Age | .49(.00)** | .14(.02)** | .14(.02)** |
| Education | -.09(.02)** | .11(.09) | .10(.09) |
| Childhood SES | -.03(.02) | .07(.13) | .07(.13) |
| Relations in family | .04(.03) | -.05(.14) | -.07 (.15) |
| Number of sexual partners | -.09(.03)** | -.05(.14) | -.04(.15) |
| Longest relationship | .13(.03)** | .56(.13)** | .16(.22) |
| Number of children | / | .90(.17)** | .93(.17)** |
| F and χ^2 (respectively) | 77.87** | 382.48** | |
| R ² | .36 | .32 | |
| Longest relationship * Sex | | | .59(.27)* |
| $\Delta \chi^2$ | | | 4.76* |
| ΔR^2 | | | .003 |

Notes: * - $p < .05$; ** - $p < .01$.

the interactions between sex and mating in the prediction of this criterion as well; however, we did not detect significant interactions.

The Number of grandchildren was predicted with the inclusion of the Number of children in the predictors set since it is a crucial covariate in the prediction of the number of grand-offspring. Participants' sex, age, Longest relationship, and the Number of children positively predicted this criterion. Furthermore, we found one significant interaction: Males with

longer relationships had more grandchildren, compared to females (Table 6 - the third column represents a regression model with interaction term included, Figure 2).

Age of First Reproduction as the Mediator Between Mating and Fitness

Finally, we conducted multigroup path analysis (for males and females separately) where we set short and long-term mating as

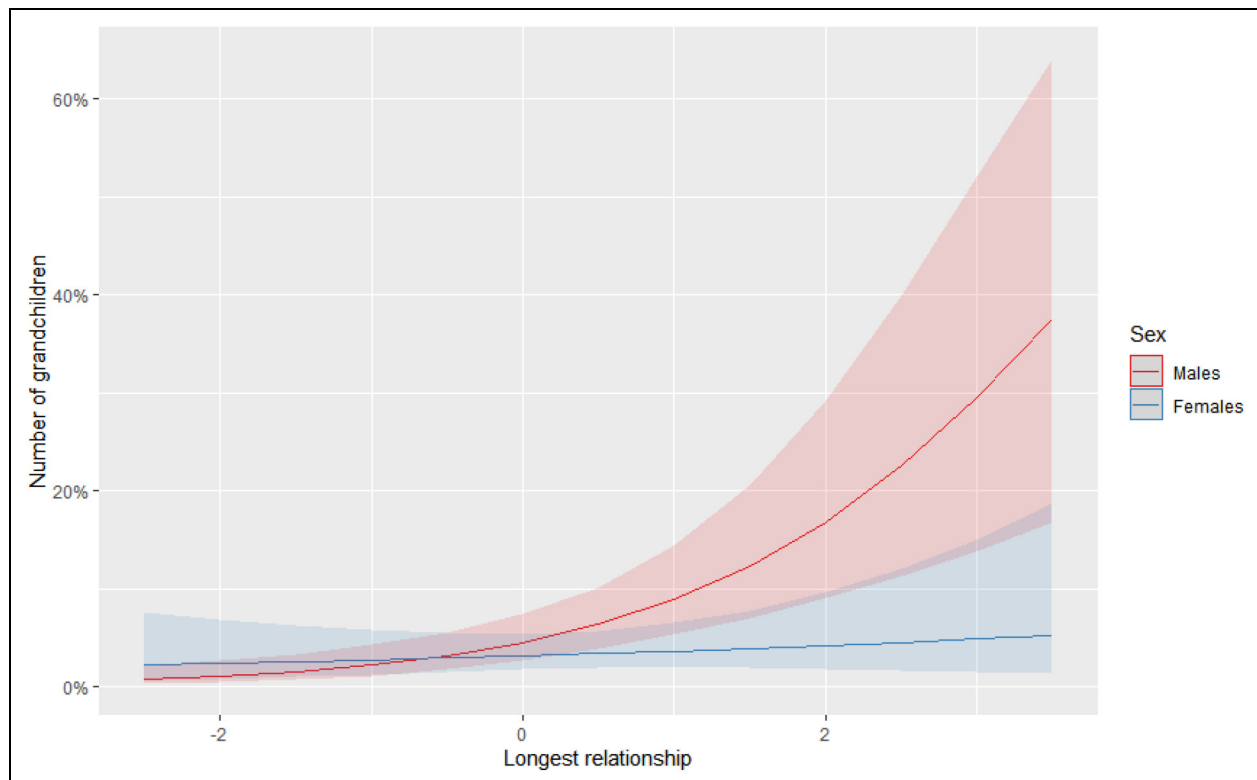


Figure 2. The interaction between sex and longest relationship in the prediction of number of grandchildren.

the predictors, the Observed age of first reproduction as the mediator, and fitness indicators (Number of children and grandchildren) as criteria variables (thus, the path analysis is performed only on participants who have children). All variables were modelled as observed ones. Note that we included age and education in the analysis as well; however, we do not show these variables in the model in order to save space. Comparisons between males and females showed significant differences in analyzed paths between the groups ($\chi^2_{(18)} = 59.76$; $p < .001$). Hence, we calculated path coefficients from subsamples of males ($\chi^2_{(3)} = 1.244$; $p > .05$; NFI = .998; CFI = 1.000; RMSEA = .004) and females ($\chi^2_{(3)} = 4.183$; $p > .05$; NFI = .991; CFI = .997; RMSEA = .033) separately and showed them on Figure 3. In general, the Observed age of first reproduction fully mediates the links between Long term mating and number of children, but only in males (standardized indirect effect: $\beta = .05$; $p < .01$). We tested the indirect effect of Long term mating on the Number of grandchildren as well, but this effect did not reach statistical significance (standardized indirect effect: $\beta = .03$; $p = .10$). The link between Longest relationship and Observed age of first reproduction was not statistically significant in females; however in this subsample there was a direct positive effect of Longest relationships on Number of children. These data are showed in Figure 3.

Discussion

The strong point of Study 2 is certainly the size of its sample and even more the fact that the sample was representative of at least some characteristics like sex, age, region, and settlement size (but not participants' education). In light of this it should be noted that all three of Bateman's observations were confirmed in this study: males had higher variance both in mating (the number of partners and longest relationship duration) and reproductive success (the number of children, grandchildren and children with multiple partners), together with a higher association

between long-term mating and the number of grandchildren. In accordance with previous data, findings showed that long-term mating is more beneficial for fitness, especially for males (Borgerhoff Mulder & Ross, 2019). Generally, the data are in accordance with the theoretical expectations and previous findings (Brown et al., 2009; Courtiol et al., 2012; Jokela et al., 2010; Moorad et al., 2011) that human males are more affected by sexual selection. However, it should be noted that only long-term mating was positively associated with fitness – in fact, multivariate analysis showed that short-term mating was negatively related to the participants' number of children; a similar result was obtained in Study 1.

The crucial reproductive event which mediates the links between short, long-term mating and fitness is reproductive timing, but only for males – the effect was not significant for female participants. The obtained mediation effect is in line with the existing empirical data regarding the mediating role of first reproduction timing in the link between long-term mating and fitness (Mededović, 2021). Males in long-term romantic relationships have earlier first reproduction; since the age of first reproduction is reliably inversely related to total reproductive success (Sanjak et al., 2018; Sheppard et al., 2016; Tropf et al., 2015), this provides these individuals with higher fitness. Certainly, the characteristics of the relationship itself are probably quite important in explaining why individuals who maintain long/term relationships earlier have their first child and have higher fitness in general, for example the perceived quality of a relationship (Rijken & Thomson, 2011), partners' positive feelings about pregnancy (Carter et al., 2013), or perceived partner's suitability to become a parent (Roberts et al., 2011). We believe that these between-partners interactions in a long-term relationship can advance future studies of the links between the long-term mating and reproductive fitness.

Similarly to the previous study, the findings regarding the life history role of mating are not clear. But yet again, the data suggest that long-term mating is involved in fast life

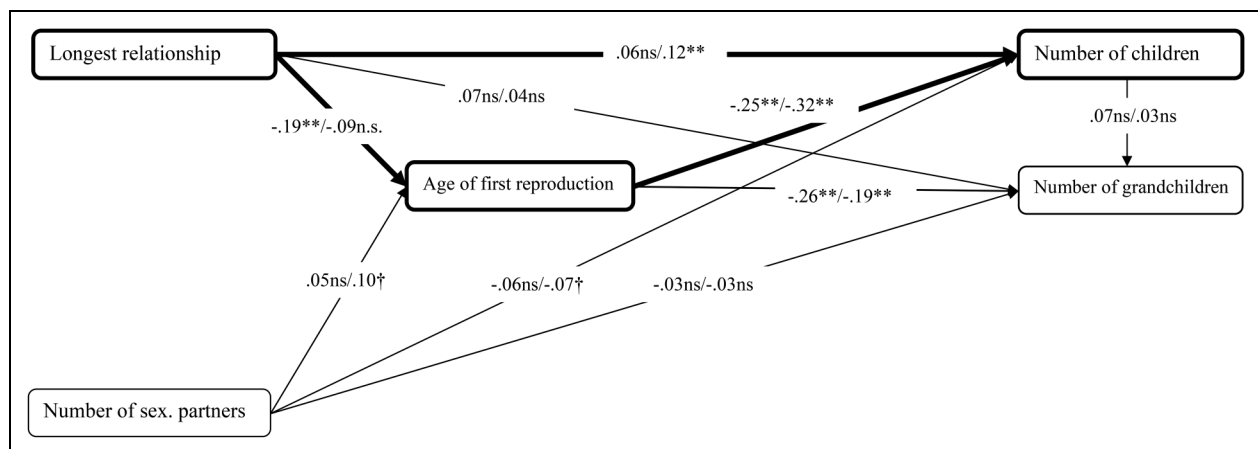


Figure 3. Path analysis of the observed age of first reproduction as a mediator between mating and fitness.

Notes: standardized coefficients are shown on the diagram; coefficients obtained in the subsample of males are shown first, coefficients obtained in the subsample of females are shown afterwards; key mediation path is shown by the bolded arrows; ns - not significant; † - $p < .10$; * - $p < .05$; ** - $p < .01$.

history dynamics: in contrast to the number of sexual partners, longer relationships are associated with maximizing reproductive output. The results from the existing research thus indirectly supported the strategic pluralism theory (Gangestad & Simpson, 2000) while they opposed developmental-attachment theory (Belsky et al., 1991) which suggested a fast life history role of short-term mating (Chua et al., 2016; Kogan et al., 2015; Lukaszewski, 2015).

General Discussion

Variation in mating behavior is certainly one of the crucial determinants of variance in fitness itself. Interestingly, the empirical data on the associations between mating and reproduction as a prerequisite for the analysis of selection regimes acting on mating, including sexual selection, are surprisingly lacking, especially in industrial and postindustrial human populations. This topic is of high importance, not only from the viewpoint of sexual selection, but life history theory in humans as well, together with the potential demographic implications. In order to explore the role of mating in reproductive ecology we conducted two studies with samples which differ in important reproductive characteristics (including the mean age of participants in two samples) and assessing different outcomes related to the environment and reproductive events. Despite the large differences between the samples the results were relatively congruent: 1) long-term mating turned out to be beneficial to fitness, while in contrast, short-term mating was either non-associated or even negatively associated to fitness; 2) long-term mating showed enhanced adaptive benefits for males compared to females; 3) age of first reproduction was the crucial mediating variable in the link between long-term mating and fitness in males; 4) short and long-term mating did not show unambiguous life history dynamics in the context of the fast/slow continuum; however, the obtained findings suggested that long-term mating had more consistent associations with the fast life history dynamics. The data show promising potential in understanding the reproductive ecology of mating in post-industrial humans as well as patterns of sexual selection in contemporary human populations.

Sexual Selection on Mating

Present findings revealed crucial differences in short and long-term mating regarding their relations with fitness: long-term mating showed more positive associations with fitness compared to short-term mating, where no relations or even negative relations with fitness were observed. In Study 1, long-term mating was positively associated with reproductive success and the total desired number of children; it was positively associated both with the number of children and grandchildren in Study 2. In both studies, longer partner relationships were related to an earlier age of first reproduction which turned out to be the crucial mediator between long-term mating and fitness for male participants. The findings that individuals with higher time spent in romantic relationships have higher fitness as well are

in accordance not only with the previous findings obtained in post-industrial, WEIRD population (Međedović, 2021) but with the data obtained in rural, natural fertility population - Pimbwe tribe of West Tanzania (Borgerhoff Mulder & Ross, 2019). In contrast, short-term mating was related to delaying reproduction in Study 1 and a lower number of children in Study 2.

We examined Bateman's three coefficients (Arnold & Duvall, 1994; Bateman, 1948) in order to estimate the presence of sexual selection: variance in mating, reproduction, and the association between mating and reproduction. Of course, we should be cautious in the interpretation of variance in mating and fertility: reliable estimations of these parameters should involve representative samples. Our samples were not representative of the Serbian population, although the sample examined in Study 2 had several characteristics of representativeness. Having in mind the problems of results generalizability, it is interesting to mention that all of the effects detected were in congruence with the sexual selection theory: the variation in mating (observed in Study 1 and 2), reproductive success (Study 2) and the finding of higher associations between mating and reproduction in males compared to females (Study 1 and 2). These findings are in accordance with several previous empirical studies (Borgerhoff Mulder & Ross, 2019; Brown et al., 2009; Courtiol et al., 2012; Jokela et al., 2010), although none one of these studies were conducted in industrial and post-industrial human populations. This is particularly interesting since theory and previous data show that sexual selection is weaker in monogamous, compared to polygamous societies (Moorad et al., 2011). Hence, although probably with lower intensity, sexual selection still operates in contemporary humans; more precisely, selection primarily acts to enhance male effort in long-term mating.

Can Mating Patterns Indicate Life History Trajectories?

Apart from sexual selection, mating patterns could be a part of human life history dynamics: correlated traits and events which are associated with fitness. Due to differences in ecological conditions and individual characteristics, humans (like other species as well) may have different pathways of fitness maximization, which are often labeled as fast and slow (Del Giudice et al., 2015). However, there are two opposite hypotheses of the role that mating patterns play in life history dynamics: one assumes that short-term mating represents a part of fast life history trajectory (Belsky et al., 1991; Chisholm, 1999), while the other posits the same role for long-term mating (Gangestad & Simpson, 2000). Both hypotheses have acquired some empirical support but it seems that there are more findings which corroborate the former one (Chua et al., 2016; Copping & Campbell, 2015; Kogan et al., 2015; Lukaszewski, 2015; Schmitt, 2005). The present data did not provide findings which may unambiguously support either of these hypotheses. However, the present data was more in line with strategic pluralism theory (Gangestad & Simpson, 2000). Short term mating showed the signatures of both fast and slow life

history while long-term mating exhibited more consistent fast life history dynamics. Indeed, the present data is in the accordance with recent predictions that long-term mating may indicate faster life history dynamics (Sear, 2020): having longer romantic relationships can facilitate reproductive success by higher frequency of sexual intercourse in steady relationships (Twenge et al., 2017) or avoiding the cost of switching partners on reproductive fitness (Brown et al., 2009).

Why were there no clearer associations between mating and life history? Well, the view of life history as a singular slow-fast dimension may be an oversimplifying framework for the analysis of human life histories. Recently, several critiques of the slow-fast life history continuum's existence have been published (Royauté et al., 2018; Stearns & Rodrigues, 2020; Zietsch & Sidari, 2020). Furthermore, empirical data showed that the latent space of life history indicators probably cannot be reduced to a single slow-fast dimension, i.e. it is much more complex and consists of several largely unrelated factors (Međedović, 2020a; 2020b; Richardson et al., 2021). The relations between the parameters of reproductive ecology and childhood environment obtained in the present study (i.e. low magnitude correlations with a high number of non-significant associations) are in contrast to the existence of a singular slow-fast continuum as well. Hence, it is questionable if this simple slow-fast life history theoretical framework is useful for understanding of the mating patterns' role in life history dynamics. This is why it has been suggested that researchers should invest more effort in linking behavioral traits (like mating patterns) with the specific life history trade-offs than trying to incorporate them in a rigid and oversimplifying fast-slow continuum (Sear, 2020).

Limitations and Future Directions

There are several important limitations of the present research. As we have already mentioned, the samples of participants the data were collected on were not representative, which limits the generalization of the data (although, the Study 2 was conducted on a large sample which was representative in several demographic parameters). The variation of the reproductive success in Study 1 was diminished which represents a potential obstacle to the generalization of the findings. Additional socio-demographic measures would be useful in the context of present topic - especially the estimate of participants' income. Participants' education levels were above the average in the present research; we can reasonably assume that the same holds for their income as well because education and economic status are positively correlated. Hence, the research findings cannot easily generalize to the participants with low education and socioeconomic status. The conducted studies were cross-sectional, which prevents causal inferences from the data; this is a limitation of previous studies in this topic as well. Despite the fact that early fertility is positively associated with completed fertility we should take the measure of reproductive success from Study 1 with caution. We did not use objective information about the participants' childhood

environment but the subjective estimations of ecological characteristics: future research may analyze objective indicators of environment like mortality rates, characteristics of the health-care system or childhood environmental instability. Furthermore, parental fitness was not controlled for in the present research; future studies should not only control for parental reproductive success but examine the parental influence on mating in offspring, since there is a parent-offspring conflict regarding the mate choice (Buunk et al., 2008).

Concluding Remarks

Mating is one of the central behaviors which influence fitness. However, previous studies on mating were relatively narrow because they explored the topics and followed methodology dominant in two principal fields of evolutionary social scientists: evolutionary psychologists were dominantly interested in the sex differences in mating strategies and neglected real-life reproductive events related to fitness; behavioral ecologists analyzed fitness (and consequently selection) but usually were limited to the number of marriages as a measure of mating. Here we tried to integrate these two frameworks in order to obtain a more comprehensive picture of mating in a reproductive ecology of the society in a demographic transition. The findings justified this strategy: they revealed fundamental differences in selection regimes on short and long-term mating; advanced our knowledge on sexual selection in humans, and initiated a new outlook on a life history of mating. The research suggested a potential complementarity of evolutionary psychology and human behavioral ecology which may be used to further advance evolutionary social sciences.

Declaration of Conflicting Interests

The author(s) declared no potential conflicts of interest with respect to the research, authorship, and/or publication of this article.

Ethical Approval

All procedures performed in studies involving human participants were in accordance with the ethical standards of the institutional and/or national research committee and with the 1964 Helsinki Declaration and its later amendments or comparable ethical standards.

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Informed Consent

Informed consent was obtained from all individual participants included in the study.

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Note

1 All administered measures are based on self-report methodology. The term "psychometric" indicates that multi-items inventories are used for the assessment; on the other hand, the term "behavioral" indicates that a concrete count measure of certain events (number of sexual partners, children or time units [months or years] is used to measure specific variable.

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